Relationships and Species Hybridization in the Genus Pinus

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A scheme of relationships within a group of plants may be of great value as a working hypothesis to guide the plant breeder. Conversely, the results of the breeder's work may be used to evaluate such a scheme and to contribute to its revision. This paper subjects two of the more important taxonomic arrangements of the genus Pinus to this process of evaluation and adjustment on the basis of the results obtained in the species hybridization program of the Institute of Forest Genetics. Supplementary evidence from biochemistry, anatomy, and morphology is adduced. Since all these studies of this large and widely distributed genus are far from complete, it is hoped that the present revision may be recognized as one of a succession of working hypotheses.

The pine hybridization program of the Institute of Forest Genetics has been sketched by Richter and Duffield (8), who discussed briefly the techniques used in recognition of hybrids. This program has depended until now on the arrangement proposed by Shaw (10) for taxonomic guidance. An arrangement by Pilger (7) is perhaps more widely known. Data on species crossabilities are now available for a comparison of the validity of these two schemes and for a tentative revision.

Since the Pilger and Shaw systems differ very little in their treatment of the sub-genus Haploxylon, and since the numerous species hybrids made in this subgenus as yet reveal no basis for relationship groupings, the present discussion is restricted to the sub-genus Diploxylon. Table 1 shows the Pilger and Shaw arrangements of the sub-genus Diploxylon. Under the Pilger system (left column) synonymy is indicated in parentheses where necessary for comparisons with Shaw system. Under the Shaw system, entities which are considered sub-species by Shaw but as species by Pilger are indented. The author accepts Pilger's interpretation of these entities as species. No attempt to bring nomenclature up to date has been made.

Table 1. — Sub-genus **Diploxylon** Koehne

Pilger (7)	Shaw (10)
Section 4. **Sula**	Sub-section **Parapinaster**
longifolia Roxb.	Group VII Leiophyllae
canariensis Smith	leiophylla Schlecht. & Cham.
Section 5. **Eupitys**	Lumholtzii Robins. & Fern.
maritima Lamk.	Group VIII Longifoliae
(pinaster Soland.)	longifolia Roxb.
tropicalis Morelet	canariensis Smith
resinosa Ait.	Group IX Pineae
Massoniana Lam.	pinea L.
densiflora Sieb. & Zucc.	Sub-section **Pinaster**
sinensis Lam.	Group X Lariciones
silvestris L.	resinosa Ait.
montana Miller	tropicalis Morelet
Merkusii Jungh.	Massoniana Lam.
Thunbergii Parl.	densiflora Sieb. & Zucc.
luchuensis Mayr	sylvestris L.
nigra Arnold	montana Miller
leucodermis Antoine	luchuensis Mayr
Section 6. **Banksia**	Thunbergii Parl.
pungens Lam.	nigra Arnold
muricata D. Don	leucodermis Antoine
Banksiana Lam.	Merkusii De Vriese
contorta Douglas	sinensis Lam.
clausa Vasey	insularis Endl.
virginiana Miller	Group XI Australes
echinata Miller	pseudostrobus Lindl.
glabra Walter	Montezumae Lam.
halepensis Miller	ponderosa Dougl.
Section 7. **Pines**	Jeffreyi Balf.
pinea L.	latifolia Sarg.
Section 8. **Australes**	arizonica Engelm.
palustris Miller	teocote Schlecht. & Cham.
caribaea Morelet	Lawsonii Roezl
occidentalis Swartz	occidentalis Swartz
Lawsonii Roezl	palustris Miller
oocarpa Schiede	caribaea Morelet
pringlei Shaw	taeda L.
Section 9. **Khasia**	glabra Walter
insularis Endl.	echinata Miller
khasya Royle	Group XII Insignes
Section 10. **Pseudostrobus**	pringlei Shaw
Lumholtzii Robins & Fern.	oocarpa Schiede
leiophylla Schlecht. & Cham.	halepensis Miller
teocote Schlecht. & Cham.	pinaster Ait.
Montezumae Lam.	virginiana Miller
pseudostrobus Lindl.	clausa Vasey
Torreyana Parry	rigida Miller
ponderosa Dougl.	serotina Michx.
Jeffreyi Balf.	pungens Lam.
Engelmannii Carr.	Banksiana Lam.
(latifolia Sarg.)	contorta Dougl.
arizonica Engelm.	Greggii Engel.
Section 11. **Taeda**	patula Schlecht. & Cham.
patula Schlecht. & Cham.	muricata D. Don
Greggii Engelm.	attenuata Lemon
serotina Michx.	radiata D. Don
rigida Miller	Group XIII Macrocarpae
taeda L.	Torreyana Parry
attenuata Lemmon	Sabiniana Dougl.
radiata D. Don	Coulteri D. Don
Sabiniana Dougl.	
Coulteri D. Don	

Figures 1 and 2 show the results of the Diploxylon crossing program with parent species arranged according to the Pilger and Shaw systems, respectively. These charts show some results obtained since the report by Righter and Duffield (8), but are simplified in several respects. Only species which have been used in attempted crosses of determinate outcome are shown. Attemps of indeterminate outcome due to recency, accidents, or insufficient data, are omitted. Crosses involving sub-specific entities are listed under the major species, e. g. crosses involving P. ponderosa var. scopulorum are not shown separately from those involving P. ponderosa. Crosses between varieties of the same species are not shown, nor are crosses involving interspecies hybrids as parents. Successful attempts are shown by solid black squares; failures by crosses. Obviously, the data on failures are of a lower order of reliability than the data on successes, for further attempts may change failures to successes, and successes are reported only for families of clearly recognizable hybrids. Only hybrids produced or grown at the Institute of Forest Genetics are shown. This means that a number of hybrids, principally between certain species native to Europe. have

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been omitted. Some of the crosses shown as failures in figs. 1 and 2, have actually been made elsewhere.

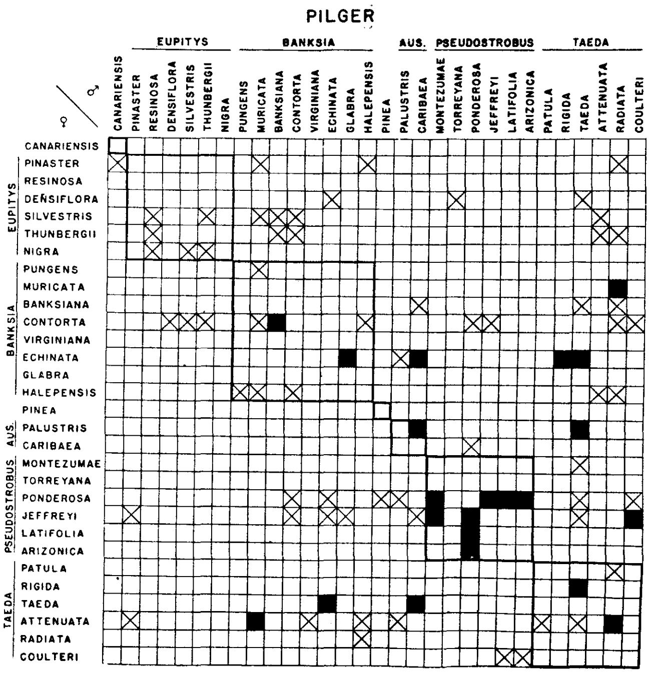

Figure 1. Crossing results at the Institute of Forest Genetics including 1948 pollinations. Parent species arranged according to Pilger (7). Solid black denotes hybrid; cross denotes failure.

(Kreuzungsresultate des Institutes für Forstgenetik bis einschließlich 1948. Elternarten angeordnet nach Pilger (7). Schwarze Felder: Bastarde; durchkreuzte Felder: mißglückte Kreuzungen.)

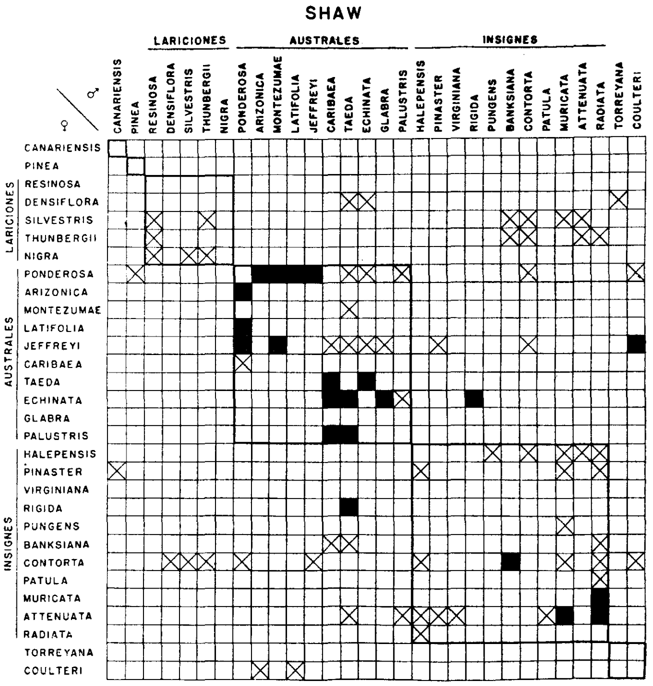

Figure 2. Crossing results at the Institute of Forest Genetics including 1948 pollinations. Parent species arranged according to Shaw (10). Solid black denotes hybrid; cross denotes failure.

(Kreuzungsresultate des Institutes für Forstgenetik bis einschließlich 1948. Elternarten angeordnet nach Shaw (10). Schwarze Felder: Bastarde; durchkreuzte Felder: mißglückte Kreuzungen.)

In figures 1 and 2, the cross-attempts within sections (Pilger) or groups (Shaw) are shown in a series of squares extending from upper left to lower right. These squares in fig. 1 (Pilger system) exclude 9 of the 22 hybrids, whereas, in fig 2 (Shaw system), only 3 of the hybrids are intersectional. Thus the crossing results obtained at the Institute agree better with Shaw's classification. This may be interpreted to mean that the Shaw system is more successful than the Pilger in showing species relationships, but it is also a consequence of the fact that a greater number of cross attempts, 54, in fact, are classified as intra-sectional under the Shaw system than under the Pilger system, which has 28. This, of course, results from the use of the Shaw system as a guide in the crossing program.

General comparisons of the validity of the two systems are not likely to be fruitful; studies of the points at which the systems break down should be more rewarding. The taxonomic principle involved here is that a given structure or character may be useful in reaching decisions about the placement of particular species, but that a large genus cannot be organized meaningfully on the basis of a single character. The general weakness of the Pilger system is the excessive reliance on needle numbers; that of the Shaw system, the over-emphasis on the asymmetrical serotinous cone.

Specific study of these two systems is further restricted to those groups in which hybrids have been produced. These are the groups Australes, Insignes, and Macrocarpae of Shaw and the sections Banksia, Australes, Pseudostrobus, and Taeda of Pilger. On the basis of crossing results, Shaw's groups Australes and Insignes appear to be too inclusive.

So far, Shaw's Australes of western North America have not been crossed with those of eastern North America. Further, the work of Mirov (4, 5, 6) has shown that the western Australes contain carene in their turpentines, while the much simpler turpentines of the eastern Australes do not contain this compound. When the species of western North America are separated from Shaw's Australes, the remaining species of eastern and southern North America and the Caribbean region form an apparently coherent group. These species, with the exception of P. occidentalis, have all been brought into crosses within the group, although not all the possible combinations have yet been attempted. On biochemical grounds too, the group is homogemeous in having rather simple turpentine consisting almost entirely of mixtures of alpha and beta pinenes (4, 5, 6). P. rigida, on the basis of crosses with P. echinata and P. taeda, should perhaps be included in this group, and this suggestion is supported by the simple oleoresin of P. rigida. Furthermore, Shaw, who placed P. rigida in his group Insignes, did so for a curious reason. He wrote of P. rigida "The cones are rarely serotinous, but it is remarkably like P. serotina in many characters, and is therefore placed in this group".

Shaw's group Insignes contains one species-complex, the California closed-cone pines, which appears to cohere on the basis of crossing results (8) and of terpene chemistry (4). Despite repeated attempts, members of this complex have not been crossed with other species included in Shaw's Insignes. The only other positive result within this group is the hybrid between P.

contorta and P. Banksiana (9). These two species have long been recognized as being quite alike in many respects, and it may, at first, seem surprising to find that their turpentines are remarkably different (4). This is another illustration of the lack of general validity of any single character. It has already been suggested that P. rigida is more closely related to the eastern species complex of SHAW's Australes than to his Insignes. Thus, the evidence accumulates that his group Insignes is an artificial composite.

When we turn to PILGER's arrangement we find the rather coherent group of eastern, southern, and Caribbean pines scattered among three sections: Banksia, Australes and Taeda. This is perhaps the clearest instance of the inadequacy of needle-numbers as a generally reliable indication of relationships. PILGER's section Australes is characterized by the position of resin canals in the needles. However, a survey of the works of SHAW (10) and HARLOW (2) fails to show that PILGER's Australes are in any way distinguishable from, e. g. P. echinata, P. taeda, or P. glabra on the basis of resin canal position.

PILGER's section Pseudostrobus appears to be a more realistic relationship grouping than SHAW's Australes for reasons already discussed. No evidence from crossing is at present available which would enable us to determine the validity of including P. Lumholtzii, P. leiophylla and P. Torreyana in the section Pseudostrobus, but there is other evidence which suggests that these species may be more realistically classified by SHAW. One may question the inclusion of P. Torreyana in PILGER's section Pseudostrobus solely, as it appears, on the basis of needle number. SHAW's inclusion of this species in his group Macrocarpae derives support from the oleoresin studies of MIROV (4), who found that the members of SHAW's Macrocarpae are unique among the Diploxylon pines in the fact that their oleoresins contain the paraffin hydrocarbons n-heptane and n-undecane (P. Jeffreyi also contains 96 percent n-heptane; this point will be dicussed later). The sub-section Parapinaster of SHAW appears to be a logical grouping, and the characters which species in this sub-section have in common are more numerous than SHAW realized. For example, all species in the sub-section Parapinaster have the triennial cone, with the possible exception of P. Lumholtzii. Furthermore, with the same possible exception, all species of this sub-section have seedlings which retain primary foliage for 2 or more years. For these reasons, PILGER's inclusion of P. Lumholtzii and P. leiophylla in section Pseudostrobus seems unwarranted.

No improvement on SHAW's Insignes can be found in PILGER's arrangement. His section Taeda is just as clearly composite even though it contains fewer species, and the same is true of his section Banksia.

What, then, can be done to rearrange the species of the sub-genus Diploxylon in a more realistic manner? Sub-division of groups — particularly SHAW's — is an obvious solution, but should not be pursued to the extreme of setting up a large number of small species complexes. This would tend to defeat one purpose of taxonomy — the elucidation of relationships. The scheme shown in Table 2 is offered as an hypothesis which can be subjected to further testing. Names for sub-generic groupings are replaced by Roman numerals to avoid confusion with previous or future arrangements, except where parts of previous arrangements are accepted unaltered.

Several of the changes evident in this table require explanation. Group X differs only slightly from the PILGER and SHAW arrangements. PILGER's section Khasya is rejected provisionally, and SHAW's inclusion of the species comprising it in the Lariciones is accepted. Admittedly there is no positive evidence to support this move, which is based on the author's low estimation of the significance of needle numbers. Biochemical evidence (MIROV, 4) does not suggest that P. Khasya differs significantly from other species in the Lariciones, while evidence on P. insularis is incomplete.

Table 2. — Sub-section **Pinaster** SHAW

Group X Lariciones ENGELM.
  P. resinosa
  P. tropicalis
  P. Massoniana
  P. densiflora
  P. silvestris
  P. montana
  P. luchuensis
  P. Thunbergii
  P. nigra
  P. Merkusii
  P. sinensis
  P. insularis
  P. khasya
  P. leucodermis
  P. halepensis
  P. pinaster
Group XI
  P. caribaea
  P. palustris
  P. echinata
  P. taeda
  P. glabra
  P. occidentalis
  P. rigida
  P. serotina
  P. pungens
Group XII
  P. teocote
  P. Lawsonii
  P. Montezumae
  P. pseudostrobus
  P. ponderosa
  P. latifolia
  P. arizonica
  P. Jeffreyi
  P. Torreyana
  P. Sabiniana
  P. Coulteri
Group XIII
  P. Banksiana
  P. contorta
  P. virginiana
  P. clausa
Group XIV
  P. radiata
  P. muricata
  P. attenuata
  P. Greggii
  P. Pringlei
  P. patula
  P. oocarpa

P. halepensis is transferred to the Lariciones on several grounds. The first of these is the position of the resin canals. HARLOW (2) has called attention to the fact that of the three positions in which resin canals are found, namely external, medial, and internal, only two of the four possible combinations of these types are found. These are medial-internal and medial-external. SHAW (10) pointed out that the external type is characteristic of Old World species of the sub-genus Diploxylon, as well as the New World species P. resinosa and P. tropicalis. When one surveys the work of HARLOW and SHAW, it becomes evident that the Lariciones may be characterized by external, medial, or medial-external resin canals, to the complete exclusion of internal or medial-internal canals. On biochemical grounds, P. halepensis fits more consistently into the Lariciones than into the Insignes of SHAW or the section Banksia of PILGER. MIROV's (4) treatment of P. halepensis is interesting. Accepting SHAW's arrangement in general, but, regarding P. pithyusa STEVEN (an entity usually considered a variety of P. halepensis) as a distinct species, he places it in the Lariciones. The oleoresins of P. halepensis and P. pithyusa were studied by two different chemists and their results are cited by MIROV, who rightly points out the great differences between the analyses reported. On purely chemical grounds, one is inclined to agree with MIROV's placement of P. pithyusa in the

Lariciones, for turpentine of this entity is reported to contain 24 percent of delta-3-carene, a compound prominent also in the turpentines of P. silvestris and P. merkusii, and not found in any of SHAW's group Insignes nor of PILGER's section Banksia. Further, P. halepensis, as reported by MIROV, contains a sesquiterpene, a class of compounds found in several species of the group Lariciones, but in none of the group Insignes nor of the section Banksia.

Despite the chemical dissimilarity between P. pithyusa and P. halepensis, it seems from morphological study that these entities are closely related, and if not conspecific, at least in the same section or group. Trees labeled P. pithyusa, growing in the Eddy Arboretum of the Institute of Forest Genetics and propagated from seed sent from the Crimea, are indistinguishable from P. halepensis var. brutia, the sessile-coned form of P. halepensis. Subsequent study may prove that P. halepensis and its variety brutia differ not only in cone attachment and seedling morphology, but in oleoresin composition as well. Finally, as evidence favoring the inclusion of P. halepensis in the Lariciones, there is the report by SVOBODA (11) of hybrids between P. halepensis and P. nigra.

Group XI is made up of the pines of the southeastern United States. These species are united on the basis of crossabilities with three exceptions: P. serotina, P. pungens, and P. occidentalis. The first two species, P. serotina and P. pungens are transferred to this group because of their morphological similarity to P. rigida — perhaps not an entirely satisfactory reason. P. occidentalis is put in this group because of its morphological similarity to the other southeastern pines.

The gounds for separating Groups XI and XII are biochemical differences and lack of crossability as already indicated. The grounds for adding to Group XII SHAW's group Macrocarpae require some comment. It has been shown that the group Macrocarpae is coherent biochemically, geographically, and morphologically. Perhaps the most striking characteristic of species in this group is the occurrence of paraffin hydrocarbons in their turpentines. Paraffin hydrocarbons are found in no other species of the sub-genus Diploxylon except P. Jeffreyi. This species, although treated by SHAW and others as a variety of P. ponderosa, might on strictly biochemical grounds be transferred to the group Macrocarpae. However, its morphological similarities to P. ponderosa are too great to permit this interpretation. Furthermore, P. Jeffreyi, crosses naturally (ZOBEL, 12) and has been crossed artifically with P. ponderosa and P. Coulteri. Therefore, provisionally, the group Macrocarpae is thrown in with the yellow pines of western North America.

Group XIII is based on the crossability of P. Banksiana and P. contorta and the morphological similarity of P. virginiana and P. clausa to the first two species. Biochemically, P. contorta stands apart from this group (MIROV, 4, 6), but the evidence from morphology and crossability is overwhelmingly in favor of its inclusion.

Group XIV remains rather unsatisfactory. It contains the coherent California closed-cone pines, and one Mexican species, P. Greggii which resembles the California closed-cone pines morphologically. Otherwise, for lack of new evidence and interpretation, this group constitutes the remains of SHAW's group Insignes.

Figure 3 shows the results of the Institute of Forest Genetics' crossing program with parent species arranged according to the proposed new scheme.

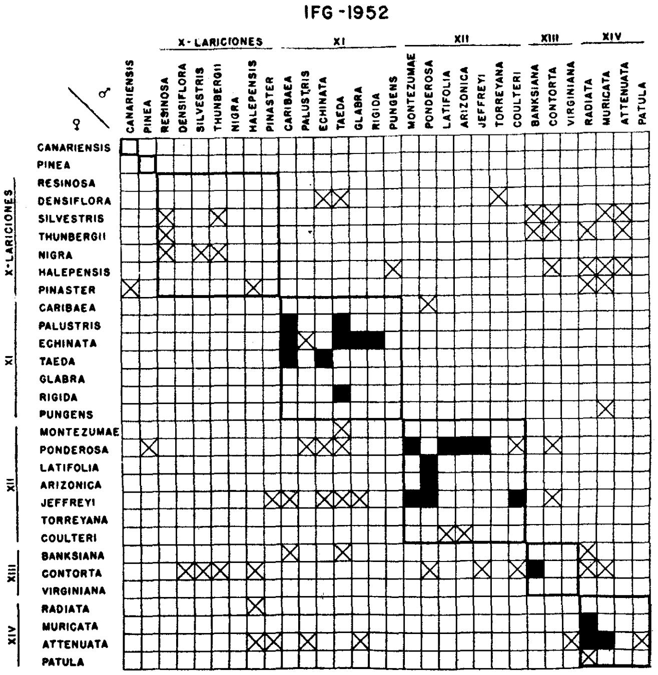

Figure 3. Crossing results at the Institute of Forest Genetics including 1948 pollinations. Parent species arranged according to proposed revision. Solid black denotes hybrid; cross denotes failure.

(Kreuzungsresultate des Institutes für Forstgenetik bis einschließlich 1948. Elternarten angeordnet nach der vorgeschlagenen Revision. Schwarze Felder: Bastarde; durchkreuzte Felder: mißglückte Kreuzungen.)

Discussion

The proposed arrangement is offered with full realization of its tentative nature, but with confidence that it represents an advance over the arrangements of PILGER and SHAW. One may rightly raise questions as to the taxonomic value of studies of crossability. Perhaps it is too much to claim that crossability data are more valuable than data on morphology, anatomy, or biochemistry, but one may claim that crossability data are at least equally valuable.

The work of CLAUSEN (1) and his co-workers, covering a number of genera of angiosperms, has resulted in a rather formal scheme of relationships based on crossability and the behavior of F_1 and F_2 hybrids. Whether this scheme is applicable to any considerable extent to the genus Pinus remains to be seen, but indications so far obtained suggest that it will not prove especially useful in this genus. For example, one may grant that the sub-genera Haploxylon and Diploxylon can be considered as different comparia, because it seems unlikely that hybrids between these two sub-genera will be obtained. However, where one views the genus Pinus against the background of the other genera in the same family, the pines appear as a well-marked, coherent group. Perhaps one should not take too literally CLAUSEN's suggestion that the comparium and the genus are equivalent. Within the sub-genus Diploxylon, as we have seen, the rigid application of the comparium concept is even less justified.

As regards the reproductive behavior of hybrids, in F_1 and F_2, the Clausen scheme again seems not to fit the pines. So far, at least 10 F_1 species hybrids have come into flower at the Institute of Forest Genetics, and none has showed more than 40 to 50 percent pollen abortion. Production of sound seed by F_1 hybrids is even better: usually at least 80 percent as good as the parent species providing pollination is adequate. Several F_2 populations have been studied, and little indication of vegetative weakness in F_2 has been found. Admittedly, only a small proportion of all the possible hybrids has been studied, but further study may support the surmise that the modes of reproduction of conifers make it impractical to apply the Clausen scheme, worked out, as it has been, on the basis of angiosperms, rigidly and in detail to the genus Pinus. Clausen's scheme may be found perfectly valid, however, if many of the entities heretofore considered species in the genus Pinus are equated to his ecospecies. Perhaps the groups of Shaw or sections of Pilger could be equated to Clausen's coenospecies. The amount of evidence at present available seems insufficient to decide these questions.

A comparison of chemical and crossing studies in the genus Pinus is of some interest because of the light it sheds on the taxonomic applications of various types of data. Lindstedt (3) has reviewed the recent investigations of the heartwood constituents of pines. He shows that the sub-genera Haploxylon and Diploxylon are clearly separated on the basis of at least four classes of compounds. Within the sub-genus Haploxylon there are rather clear differences between species and groups of species. Within the sub-genus Diploxylon, there is great uniformity in heartwood constituents. Thus this type of study has a different value in different subgenera just as is the case with crossability data, which are much less useful in Haploxylon than in Diploxylon. The volatile constituents of oleoresin (Mirov, 4) do not show a sharp separation between Haploxylon and Diploxylon, but within both sub-genera, are of considerable interest in separating certain species pairs and in uniting certain species groups. Therefore, it seems that any extensive taxonomic arrangement cannot rely exclusively on any single type of information.

From the point of view of the pine breeder, a taxonomic scheme which takes crossabilities into account should have practical interest. Numerous students of the pines have been impressed with the ecological and morphological similarities between P. silvestris on one hand and P. contorta and P. Banksiana on the other. Attempts to cross P. silvestris with these two North American species should and will be made. Nevertheless, from the viewpoint expressed in this paper, such attempts seem less likely to succeed than many others which might produce hybrids of considerable value and interest. No doubt some crosses which now are difficult or impossible will be facilitated by advances in techniques, but in the meantime, it would seem that the best use of the tree breeder's limited resources would be directed first toward crossing species which, on the basis of available evidence, show the greatest probability of being readily crossable.

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Verwandtschaftsverhältnisse und Artkreuzungen in der Gattung Pinus

Von J. W. Duffield

(Autorisierte Übersetzung vorstehender Originalarbeit*)

Ein Schema über verwandtschaftliche Beziehungen innerhalb einer Gruppe von Pflanzen ist für den Züchter als Arbeitshypothese von größtem Wert. Umgekehrt können Züchtungsergebnisse zur Auswertung und Revision eines solchen Schemas benutzt werden. Die in der vorliegenden Veröffentlichung mitgeteilten Ergebnisse des Artkreuzungsprogramms des Institutes für Forstgenetik ermöglichen dies bei zwei der wichtigsten taxonomischen Einteilungen der Gattung Pinus. Zusätzlich werden Hinweise aus Biochemie, Anatomie und Morphologie herangezogen. Obgleich der Abschluß dieser Studien bei dieser umfangreichen und weitverbreiteten Gattung noch aussteht, ist zu hoffen, daß womöglich die vorgelegte Revision als ein Erfolg der gewählten Arbeitshypothese angesehen werden kann.

Das Kiefernkreuzungsprogramm des Institutes für Forstgenetik wurde von Righter und Duffield (8) aufgestellt, die kurz über die Erkennbarkeit der Bastarde berichteten. Dieses Programm benutzte die von Shaw (10) vorgeschlagene taxonomische Einteilung. Bekannter ist wahrscheinlich die Einteilung nach Pilger (7). Nunmehr sind Ergebnisse über Kreuzbarkeit von Arten verfügbar, die einen Vergleich der beiden Schemata und ihre eventuelle Revision gestatten.

Da sich Pilgers und Shaws System nur wenig in der Behandlung der Untergattung (Subgenus) Haploxylon unterscheiden und da die zahlreichen Artbastarde, die in dieser Untergattung hergestellt wurden, bisher noch nicht als Grundlage für verwandtschaftliche Gruppierungen dienen können, beschränkt sich der vorliegende Bericht auf die Untergattung Diploxylon. Tafel 1 zeigt die Einteilung dieser Untergattung nach Pilger und Shaw. In der Spalte Pilger (links) wurden die Synonyme, wenn es zum Vergleich mit Shaws System nötig war, in Klammern gesetzt. In der Spalte Shaw (rechts) sind systematische Stufen, die bei Shaw als Unterarten, bei Pilger als Arten bezeichnet

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*) Übersetzt von Z. M. Illies, Schmalenbeck.